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RELATIONSHIP BETWEEN RAPTORS AND RABBITS IN THE DIET OF EAGLE OWLS IN SOUTHWESTERN EUROPE: COMPETITION REMOVAL OR FOOD STRESS?

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ABSTRACT.—I tested whether higher predation rates by Mediterranean Eagle Owls (*Bubo bubo*) on other species of raptors was associated with lower availability of the most profitable prey for this owl, the European rabbit (*Oryctolagus cuniculus*). Additionally, I investigated whether the main force regulating the importance of raptors in the diet of Eagle Owls was the acquisition of food or the removal of competition. Rabbits are the staple prey of this species in Mediterranean ecosystems of southwestern Europe. My analysis was based on 17 557 prey items from 19 studies of Eagle Owl diet in Spain and France. Rabbits and raptors showed significant inverse relationships, but this trend was not significant when only raptors competing for rabbits were included in the analysis. Thus, trophic diversification when rabbit numbers were low, including changes in the use of the foraging habitat, seemed to be the main explanation for this interaction. Rabbit populations have declined sharply after two outbreaks of viral diseases that have been linked to an increase of other raptors in the diet of Eagle Owls. For this reason, the management of rabbits could benefit the conservation of raptor communities, of which eagle owls are a part.

KEY WORDS: *Eagle Owl*, Bubo bubo; *food stress*; *intraguild predation*; *European rabbit*; Oryctolagus cuniculus; *Mediterranean.*

Relación entre aves rapaces y conejos en la dieta de *Bubo bubo* en el suroeste de Europa: competencia por remoción o estres por alimento?

RESÚMEN.—Se exploraron las relaciones entre el conejo (*Oryctolagus cuniculus*) y el resto de las rapaces en la dieta del búho real (*Bubo bubo*) en ecosistemas mediterráneos del suroeste de Europa. Asimismo, se intentó determinar si dicha relación responde simplemente a una búsqueda de presas alternativas o a la eliminación de competidores. Se recopiló bibliografía que incluía 17 557 presas pertenecientes a 19 poblaciones de España y Francia. Fueron halladas correlaciones significativas que relacionaban de forma inversa la contribución de rapaces y conejos a la dieta del ave. Sin embargo, al incluir en los análisis únicamente aves rapaces que pueden competir por el conejo las tendencias no fueron significativas. Se concluyó que existe una respuesta funcional de los búhos reales en áreas con bajos niveles poblacionales de conejo y que la diversificación de la dieta y los cambios en el uso del hábitat de caza, y no la eliminación de competidores, parecen las explicaciones más plausibles para este tipo de interacción. Las densidades de conejo han sufrido un acentuado declive como consecuencia de la mixomatosis y de la neumonía hemorrágica vírica que parece estar determinando una mayor importancia de las rapaces en la dieta de los búhos. Consecuentemente, un adecuado manejo de las poblaciones de conejo podría redundar indirectamente en la conservación de las aves de presa que comparten hábitat con el búho real.

[Traducción del autor]

The role of top predators on food-web structure and predator-prey interactions may have strong implications in conservation and management of both game-species and predator assemblages (Palomares et al. 1995, Litvaitis and Villafuerte 1996). In this sense, raptors killing other raptors has been suggested to affect the structure and other aspects of population dynamics in bird of prey communities (Mikkola 1976, Rudolph 1978, Hakkarainen and Korpimäki 1996). This ecological process is particularly important when it involves individuals of endangered species as prey, a case in which the death of a few individuals may drive local populations to extinction. There is uncertainty about

whether raptors kill other raptors simply to acquire food or to obtain benefits by removing competitors (Mikkola 1983, Rohner and Doyle 1992). Although experiments are needed, these are difficult with such wide-ranging species. Therefore, analysis of existing empirical data should be encouraged.

Eagle Owls (*Bubo bubo*) are large nocturnal raptors preying on a wide spectrum of species, both in terms of body size and ecological requirements. European rabbits (*Oryctolagus cuniculus*) constitute the preferred prey of this species in Mediterranean habitats of southwestern Europe due to their abundance and the absence of other prey of similar size (Hiraldo et al. 1976, Jaksić and Marti 1984, Donázar et al. 1989). However, rabbit densities vary between areas, specially after outbreaks of viral diseases that have reduced populations (Villafuerte et al. 1995). Eagle Owls feed preferentially on this species in Mediterranean areas whenever it is abundant, but switch to less profitable alternative prey where rabbits are scarce. Thus, rabbit occurrence in the owl's diet may indicate their local availability (Donázar 1989, Serrano 1998).

Numerous studies of Eagle Owls have shown the regular occurrence of raptors in their diet (see review in Mikkola 1983, Penteriani 1996), including young and adults of threatened species (Real and Mañosa 1990, Tella and Mañosa 1993). Eagle owls may act as both predators and competitors with other raptors at a similar trophic level, so intraguild predation (*sensu* Polis and Holt 1992) could be an explanation for such an interaction. Alternatively, it has been suggested that Eagle Owls in Mediterranean ecosystems feed on a larger proportion of raptors in conditions of food stress resulting from rabbit scarcity (Tella and Mañosa 1993). This hypothesis requires more study of different populations of raptors and their prey to provide additional evidence. If raptors actually compete with Eagle Owls (i.e., those feeding on rabbits are killed when rabbits are scarce), an inverse relationship should occur between their dietary proportions. Alternatively, if food stress as a consequence of rabbit scarcity is the main explanation for Eagle Owls killing other raptors, there should be no relationship between the proportion of raptors competing for food and rabbits in their diet. Thus, studying the dietary contribution of raptors in different scenarios of rabbit availability could improve our understanding of interspecific depredation among raptors. The aim of this paper was to quantify the importance of raptors in the diet of Mediterranean Eagle Owls and to explore whether higher predation rates on other raptor species are associated with lower availability of rabbits. Additionally, two hypothesis were tested: whether food stress or competition removal is the main force regulating this phenomenon.

METHODS

This paper is based on 19 studies of Eagle Owl diet in Spain and France, which included >200 prey items per study (Table 1). Most of these studies used the analysis of pellets from nestlings and adults to determine the diet which seems to accurately reflect overall owl diet. Numerical and biomass contribution were reported since frequency is important when looking at the number of competitors removed and biomass reflects the energetic yield of each taxonomic group. Percent biomass of each taxonomic group in the diet were calculated following Hiraldo et al. (1975a), Real et al. (1985), and Perrins (1987). A value of 500 g was assigned to each rabbit, as Eagle Owls actively select young and subadult rabbits (Donázar and Ceballos 1989).

Falconiformes are active diurnally, whereas Strigiformes are mainly nocturnal, and frequently share foraging habitats with Eagle Owls. Moreover, nocturnal raptors can be potentially detected by Eagle Owls through their vocalizations. Thus, for statistical analysis, Falconiformes and Strigiformes were considered as two separate groups

RESULTS

Falconiformes and Strigiformes comprised 97 (0.55%) and 223 (1.27%) out of the 17 557 prey items identified. Biomass frequencies were 0.7 and 1.0%, respectively. This included the depredation of 10 species of Falconiformes and six of Strigiformes (Table 2), although at least four other species of Falconiformes (Egyptian Vulture [*Neophron percnopterus*], Bonelli's Eagle [*Hieraaetus fasciatus*], Booted Eagle [*Hieraaetus pennatus*], and Red Kite [*Milvus milvus*]) have also been reported to be prey of Eagle Owls in Mediterranean ecosystems of Europe (Pérez-Chiscano 1974, Real and Mañosa 1990, Tella and Mañosa 1993). European Kestrels (*Falco tinnunculus*) were the most frequently taken Falconiform, while Little (*Athene noctua*) and Barn (*Tyto alba*) Owls were the most commonly taken Strigiforms (Table 2).

Frequency of occurrence of diurnal raptors and rabbits was negatively related ($r_s = -0.61$, $N = 19$, $P = 0.006$), but this trend was not significant for nocturnal raptors ($r_s = -0.39$, $N = 19$, $P = 0.103$). The contribution of raptor and rabbit biomass to the owl diet was negatively related when analyzed separately (Falconiformes: $r_s = -0.65$, $P = 0.002$; Strigiformes: $r_s = -0.55$, $N = 19$, $P = 0.014$). These results could have been due to the high biomass

Table 1. Numerical (N) and Biomass (B) frequencies of Falconiformes (Falc), Strigiformes (Stri), and European rabbits (Rabb) in 19 populations of Mediterranean Eagle Owls. Sample sizes in each population is given (*N*).

	Falc		Stri		Rabb			
Locality	N	B	N	B	N	B	*N*	Reference
Bardenas	0	0	3.7	2.0	64.1	85.1	245	1[a]
Navarra E	0.4	0.7	3.3	2.6	22.7	46.1	958	1[a]
Navarra W	0.3	1.6	1.6	2.5	10.2	26.9	1355	1[a]
Ebro N	0.4	1.6	0.9	2.9	5.2	31.3	2141	2[a]
Ebro S	0.8	1.2	1.9	1.3	33.5	65.5	1529	2[a]
Murcia	1.4	0.8	1.5	0.6	53.6	66.0	1398	3[b]
Toledo 1	0.1	0.3	0	0	79	77.5	829	4[b]
Villuercas	0.3	0.9	0	0	42.4	57.4	361	4[b]
Málaga	0	0	0	0	61.3	77.6	256	5[b]
S. Morena	0.2	0.2	0.2	0.1	67.9	76.1	1590	5[b]
Extremadura	0.2	0.6	0.5	0.4	41.2	53.2	417	5[b]
Toledo 2	0	0	0.7	0.3	77.1	83.6	266	5[b]
Salamanca	0.7	1.2	0.1	0.1	25.8	43.3	732	5[b]
Massif Central	3.2	4.2	6	4.7	15.3	19.0	216	6[b]
Tarn	1	0.6	1.5	1.0	22.8	25.4	595	7[b]
Hérault	0.5	1.0	1.4	1.2	26.5	39.2	623	7[b]
Provence 1	0.6	0.4	1.4	1.4	19	31.2	2923	8[b]
Vallès	0.3	0.4	0.1	0.3	22.1	34.5	724	9[b]
Provence 2	0.2	0.2	1.5	0.9	35.8	45.9	399	10[b]

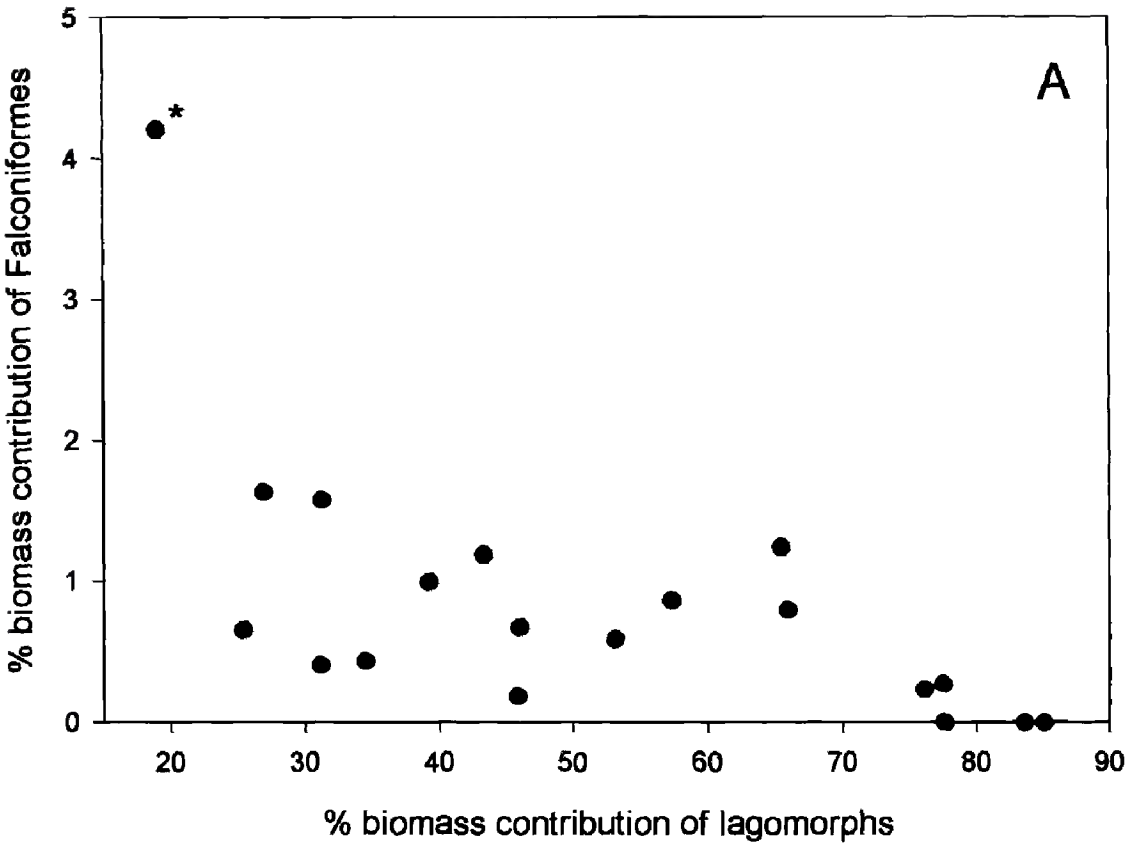
1 Donázar 1989; 2: Serrano 1998; 3: Martínez et al. 1992; 4: Pérez-Mellado 1980; 5: Hiraldo et al. 1975b; 6: Choussy 1971; 7: Cugnasse 1983; 8: Orsini, 1985; 9: Real et al. 1985; 10: Blondel and Badan 1976.

[a] Pellet remains from adults.

[b] Pellet remains from adults and nestlings.

Table 2. Number of raptors (*N*) and numerical (%N) and biomass (%B) frequencies of each species of raptor taken by Eagle Owls in 19 Mediterranean populations. Species competing with Eagle Owls for rabbits are shown (*).

Species		*N*	%N	%B
Falco tinnunculus		64	20.0	13.2
Falco peregrinus		1	0.3	1.0
Accipiter nisus		4	1.3	0.7
Accipiter gentilis	(*)	2	0.6	2.4
Circus aeruginosus	(*)	1	0.3	0.6
Circus pygargus		4	1.3	1.2
Buteo buteo	(*)	10	3.1	9.8
Milvus migrans	(*)	5	1.6	5.1
Pernis apivorus		1	0.3	0.9
Circaetus gallicus		1	0.3	2.1
Unidentified Falconiforms		4	1.3	4.1
Tyto alba		76	23.7	23.4
Strix aluco		28	8.7	12.9
Athene noctua		88	27.5	15.4
Asio otus		23	7.2	6.5
Otus scops		8	2.5	0.7
Total		320	100	100



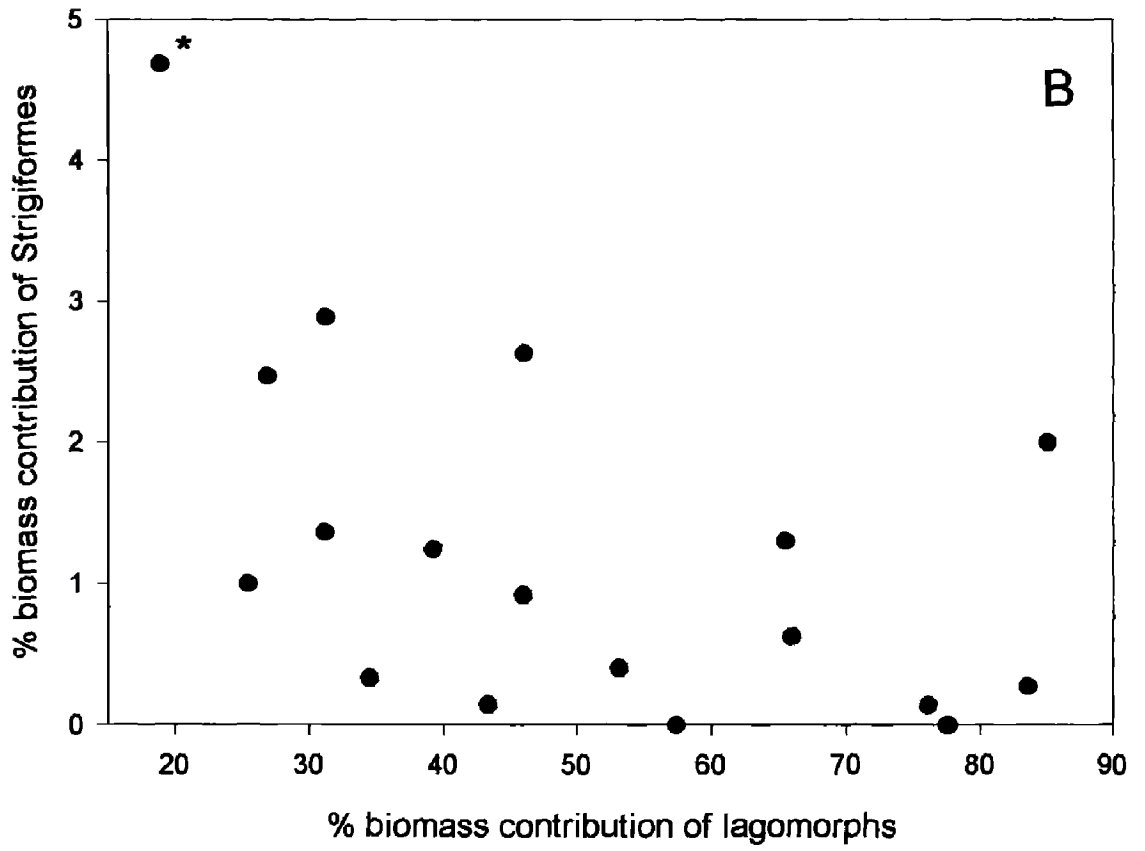


Figure 1. Percent biomass of lagomorphs in relation to percent biomass of Falconiformes (A) and Strigiformes (B) in the diet of 19 populations of Eagle Owls (*Bubo bubo*) in western Palearctic. The symbol * shows the population of Massif Central.

of raptors in the study from the Massif Central (Fig. 1). Removing this sample from the analysis reduced the strength of the relationships, but they were still significant (Falconiformes: $r_s = -0.59$, $P = 0.009$; Strigiformes: $r_s = -0.47$, $N = 19$, $P = 0.049$). Only four species of Falconiformes in these studies may compete with Eagle Owls for rabbits (Table 2; see del Hoyo et al. 1994). After removing the rest from the analysis, the relationship was not maintained when raptor and rabbit contribution

was analyzed (numerical frequencies: $r_s = -0.17$, $N = 19$, $P = 0.484$; biomass frequencies: $r_s = -0.32$, $N = 19$, $P = 0.181$).

DISCUSSION

My results suggest a close relationship between rabbits, the main prey, and raptors in the diet of Eagle Owls. This agreed with Tella and Mañosa (1993) who found that Eagle Owls seemed to take a larger proportion of raptors when rabbits were scarce. The weak relationship between rabbits and raptors competing for food with Eagle Owls suggested a food-searching rather than a competitor-removal process. Moreover, the fact that the species most frequently taken seldom compete for trophic resources with Eagle Owls supported this hypothesis.

Rabbits are social mammals inhabiting flat or gently undulated Mediterranean scrub habitats of the western Palearctic. In areas of high density of rabbits, Eagle Owls seem to concentrate their hunting effort in distinct perches around burrows. In contrast, other types of habitat are exploited in areas with low rabbit densities (Serrano 1998). Eagle Owls discriminate prey by size rather than by a taxonomic criterion, and are capable of killing most Mediterranean raptors. Thus, when rabbits are scarce, Eagle Owls probably search for alternative prey more frequently in habitats used by other raptors for nesting or roosting (e.g., cliffs, woodlands, and river groves). Thus, an increase of raptors in the diet is related to diet diversification as a consequence of low rabbit abundance (see Hiraldo et al. 1976, Donázar et al. 1989, Serrano 1998 for changes in trophic diversity according to rabbit availability).

Rabbits constitute one of the staple food sources for the top predator assemblage of Mediterranean ecosystems in western Europe (Delibes and Hiraldo 1981). Thus, the decline of European rabbits in recent decades as a consequence of human-induced epizootic diseases (first myxomatosis, see Delibes and Hiraldo 1981, and then viral haemorrhagic disease, Villafuerte et al. 1995) has been suggested to affect some threatened species of raptors (e.g., Fernández 1993, Garza and Arroyo 1996, González 1996, Villafuerte et al. 1998, but see Ontiveros and Pleguezuelos 2000). Regardless of the low incidence of raptors in the overall diet of Eagle Owls, my results indicated that low rabbit populations could be influencing the structure of Mediterranean raptor communities and the conservation of endangered sympatric raptors. In this sense, preliminary results of an ongoing research carried out in eight study areas in the Italian pre-Alps have highlighted a significant effect of Eagle Owl abundance on the pattern of nest dispersion, territory occupation, and productivity of some species in the diurnal raptor assemblage (Sergio et al. 1999a, 1999b). However, to determine the abundance and distribution of other raptors in relation to Eagle Owl diet and rabbit abundance, additional research is needed to assess the impact of this top predator on raptor communities.

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LITERATURE CITED

BLONDEL, J. AND D.O. BADAN. 1976. La biologie du Hibou Grand Duc en Provence. *Nos Oiseaux* 33:189–219.

CUGNASSE, J.M. 1983. Contribution a l'etude de Hibou Grand Duc (*Bubo bubo*) dans le sud Massif Central. *Nos Oiseaux* 37:117–128.

CHOUSSY, F. 1971. Etude d'une population de Grand Duc (*Bubo bubo*) dans le Massif Central. *Nos Oiseaux* 31:37–56.

DEL HOYO, J., A. ELLIOTT, AND J. SARGATAL. 1994. Handbook of the birds of the world. Vol. 2. New World vultures to guineafowl. Lynx Edicions, Barcelona, Spain.

DELIBES, M. AND F. HIRALDO. 1981. The rabbit as prey in the Iberian Mediterranean ecosystem. Pages 614–622 *in* K. Myers and C.D. McInnes [EDS.], Proceedings of the world lagomorph conference. Univ. Guelph, Guelph, Ontario, Canada.

DONÁZAR, J.A. 1989. Variaciones geográficas y estacionales en la alimentación del Búho Real (*Bubo bubo*) en Navarra. *Ardeola* 36:25–39.

———, F. HIRALDO, M. DELIBES, AND R.R. ESTRELLA. 1989. Comparative food habits of the Eagle Owl *Bubo bubo* and the Great Horned Owl *Bubo virginianus* in six Palearctic and Nearctic biomes. *Ornis Scand.* 20:298–306.

——— AND O. CEBALLOS. 1989. Selective predation by Eagle Owls *Bubo bubo* on rabbits *Oryctolagus cuniculus*: age and sex preferences. *Ornis Scand.* 20:117–122.

FERNÁNDEZ, C. 1993. Effect of the viral haemorrhagic pneumonia of the wild rabbit on the diet and breeding success of the Golden Eagle *Aquila chrysäetos* (L.). *Rev. Ecol. Terre Vie* 48:323–329.

GARZA, V. AND B. ARROYO. 1996. Situación del Águila perdicera (*Hieraaetus fasciatus*) en España. Pages 219–229 *in* J. Muntaner and J. Mayol [EDS.], Biology and conservation of Mediterranean raptors, 1994. Monografía No. 4. SEO-BirdLife, Madrid, Spain.

GONZÁLEZ, L.M. 1996. Tendencias poblacionales y estatus

de conservación del Águila Imperial Ibérica (*Aquila adalberti*) en España durante los últimos 20 años. Pages 61–75 *in* J. Muntaner and J. Mayol [EDS.], Biology and conservation of Mediterranean raptors, 1994. Monografía No. 4. SEO-BirdLife, Madrid, Spain.

HAKKARAINEN, H. AND E. KORPIMÄKI. 1996. Competitive and predatory interactions among raptors: an observational and experimental study. *Ecology* 77:1134–1142.

HIRALDO, F., F. FERNÁNDEZ, AND F. AMORES. 1975a. Diet of the Montagu's Harrier (*Circus pygargus*) in southwestern Spain. *Doñana Acta Vertebrata* 2:25–55.

———, J. ANDRADA AND F.F. PARREÑO. 1975b. Diet of the Eagle Owl (*Bubo bubo*) in Mediterranean Spain. *Doñana Acta Vertebrata* 2:161–177.

———, F.F. Parreño, V. Andrada, and F. Amores. 1976. Variations in the food habits of the European Eagle Owl(*Bubo bubo*). *Doñana Acta Vertebrata* 3:137–156.

JAKSIĆ, F.M. AND C.D. MARTI. 1984. Comparative food habits of *Bubo* owls in Mediterranean-type ecosystems. *Condor* 86:288–296.

LITVAITIS, J.A. AND R. VILLAFUERTE. 1996. Intraguild predation, mesopredator release, and prey stability. *Conserv. Biol.* 10:676–677.

MARTÍNEZ, J.E., M.A. SÁNCHEZ, D. CARMONA, J.A. SÁNCHEZ, A. ORTUÑO, AND R. MARTÍNEZ. 1992. The ecology and conservation of the Eagle Owl *Bubo bubo* in Murcia, south-east Spain. Pages 84–88 *in* C.A. Galbraith, I.R. Taylor, and S. Percival [EDS.], The ecology and conservation of European owls. U.K. Nature Conservation No. 5. Joint Nature Conservation Committee, Peterborough, U.K.

MIKKOLA, H. 1976. Owls killing and killed by other owls and raptors in Europe. *Br. Birds* 69:144–154.

———. 1983. Owls of Europe. Poyser, Berkhamsted, U.K.

ONTIVEROS, D. AND J.M. PLEGUEZUELOS. 2000. Influence of prey densities in the distribution and breeding success of Bonelli's Eagle (*Hieraaetus fasciatus*): management implications. *Biol. Conserv.* 93:19–25.

ORSINI, P. 1985. Le régime alimentaire du Hibou Grand-duc *Bubo bubo* en Provence. *Alauda* 53:11–28.

PALOMARES, F., P. GAONA, P. FERRERAS, AND M. DELIBES. 1995. Positive effects on game species of top predators by controlling smaller predator populations: an example with lynx, mongooses, and rabbits. *Conserv. Biol.* 9:295–305.

——— AND T.M. CARO. 1999. Interspecific killing among mammalian carnivores. *Am. Nat.* 153:492–508.

PENTERIANI, V. 1996. The Eagle Owl. Calderini Edagricole, Bologne, Italy. (In Italian)

PÉREZ-CHISCANO, J.L. 1974. Sumario informe sobre la alimentación de rapaces en el nor-este de la provincia de Badajoz. *Ardeola* 19:331–336.

PÉREZ-MELLADO, V. 1980. Alimentación del Búho Real (*Bubo bubo* L.) en España Central. *Ardeola* 25:93–112

PERRINS, C. 1987. Aves de España y Europa. Omega, Barcelona, Spain.

POLIS, G.A. AND R.D. HOLT. 1992. Intraguild predation: the dynamics of complex trophic interactions. *Tree* 7: 151–154.

REAL, J., A. GALOBART, AND J. FERNÁNDEZ. 1985. Estudi preliminar d'una població de Duc (*Bubo bubo*) al Vallès i Bages. *Medi Natural del Vallès*:175–187.

——— AND S. MAÑOSA. 1990. Eagle Owl (*Bubo bubo*) predation on juvenile Bonelli's Eagles (*Hieraaetus fasciatus*). *J. Raptor Res.* 24:69–71.

ROHNER, C. AND F.I. DOYLE. 1992. Food-stressed Great Horned Owl kills adult goshawk: exceptional observation or community process? *J. Raptor Res.* 26:261–263.

RUDOLPH, S.G. 1978. Predation ecology of coexisting Great Horned and Barn Owls. *Wilson Bull.* 90:134–137.

SERRANO, D. 1998. Diferencias interhábitat en la alimentación del Búho Real (*Bubo bubo*) en el valle medio del Ebro (NE España): efecto de la disponibilidad de conejo (*Oryctolagus cuniculus*). *Ardeola* 45:47–53.

SERGIO, F., L. MARCHESI, P. PEDRINI, AND F. RIZZOLLI 1999a. Il Gufo reale *Bubo bubo* come potenziale fattore limitante per tre specie di rapace diurni. *Avocetta* 23: 113.

———, L. MARCHESI AND P. PEDRINI. 1999b. Black Kite (*Milvus migrans*) density and productivity in relation to predation pressure by the Eagle Owl (*Bubo bubo*) *Buteo* (Suppl.):30.

TELLA, J.L. AND S. MAÑOSA. 1993. Eagle Owl predation on Egyptian Vulture and Northern Goshawk: possible effect of a decrease in European rabbit availability. *J. Raptor Res.* 27:111–112.

VILLAFUERTE, R., C. CALVETE, J.C. BLANCO, AND J. LUCIENTES. 1995. Incidence of viral hemorrhagic disease in wild rabbit populations in Spain. *Mammalia* 59:651–659.

———, J. VIÑUELA, AND J.C. BLANCO. 1998. Extensive predator persecution caused by population crash in a game species: the case of Red Kites and rabbits in Spain. *Biol. Conserv.* 84:181–188.

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